TRANSPIRATION OF SUN LEAVES AND SHADE LEAVES OF OLEA EUROPAEA AND OTHER BROAD-LEAVED EVERGREENS.

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(WITH ELEVEN FIGURES)

THE structural differences between sun leaves and shade leaves of several species have been described in a classical memoir by E. STAHL.[1] FR. JOHOW has given an excellent summary of the adaptations of foliage leaves with reference to transpiration.[2] LEON DUFOUR has investigated many of the differences in the vegetative and the reproductive organs of phanerogams due to differences in the amount of light supplied to them.[3]

The writer has not at present access to any tolerably complete collection of botanical periodicals, but neither in ALFRED BURGERSTEIN'S bibliography[4] nor in such journals as were accessible has he been able to find mention of any paper which discusses experimentally the subject of transpiration *in leaves of the same individual*, some developed in the sun and others in the shade. It would seem that the study of the relative activity of sun leaves and shade leaves must give results of value. For such an investigation no leaves can be more suitable than those of such evergreens as the Mediterranean species of what Schimper calls the *Hartlaubflora*, Olea, *Quercus Ilex*, Myrtus, and their congeners. For it is evident that leaves which are active during a period of from one to several years, and which during all of that period are respectively exposed to illuminations varying from 2 per cent. to 100 per cent. of the total amount afforded by the sun, may be expected to show far more notable differences in structure

[1] Einfluss des sonnigen oder schattigen Standortes auf die Ausbildung der Laubblätter. Jena. Zeits. Naturwiss. **16**:162. 1882.

[2] Ueber die Beziehungen einiger Eigenschaften der Laubblätter zu den Standortsverhältnissen. Jahrb. Wiss. Bot. **15**:—. 1884.

[3] Influence de la lumière sur la forme et la structure des feuilles. Ann. Sci. Nat. Bot. VII. **5**:311–412. 1887.

[4] Materialien zu einer Monographie der Transpiration der Pflanzen. Verhandl. Zoöl.-Bot. Gesells. Wien. 1887 and 1899.

and function, due to unequal illumination, than those leaves which flourish only for four or five months of the year. Broad-leaved evergreens, too, cast a denser shade than is afforded by ordinary conifers, and the leaves of the former therefore grow under more sharply contrasting conditions than do those of the latter.

The lack of suitable laboratory facilities has made it impossible for the writer to investigate the relative amounts of photosynthesis accomplished by the leaves of the species studied. It has been possible, however, to determine with a fair degree of accuracy the relative amount of transpiration done by the sun leaves and the shade leaves of several species.

The trees and shrubs mostly studied were: *Olea europaea sativa*, *Pistacia Lentiscus*, *Quercus Ilex*, and *Rhamnus Alaternus*. The observations, unless otherwise stated, were made upon leaves from thirteen to fifteen months old. Where sun leaves and shade leaves were compared these were from different parts of the same shrub or tree, those which received only part of the total illumination being shaded wholly by their own foliage.

I. COMPARISONS OF COLOR, SIZE, SHAPE, AND STRUCTURE OF SUN LEAVES AND SHADE LEAVES.

Out of ten trees and shrubs examined with reference to the effect of illumination on the color of the upper surface of the leaf, only one, *Quercus Ilex*, showed sun leaves always darker than the shade leaves. In this species the sun leaves when fully matured were always found to be of a very dark green, while shade leaves (1 to 2 per cent. illumination) were of a grass-green color.

Buxus sempervirens showed no perceptible difference in color due to difference in illumination.

Eight species (*Arbutus Andrachne*, *A. Unedo*, *Citrus Aurantium*, *Myrtus communis tarentina*, *Nerium Oleander*, *Olea europaea*, *Pistacia Lentiscus*, *Rhamnus Alaternus*) showed a much darker tint of green in the shade leaves than in the sun leaves, though sometimes the shade leaves of Pistacia are lighter green. The shade leaves in the individuals studied received amounts varying from 1 to 10 per cent. of the total illumination.

In comparing the relative areas of sun leaves and shade leaves,

the author arrives at a result opposite to that which DUFOUR[5] obtained from the study of many herbaceous species, but agreeing with the results of JOHOW.[6]

One species, *Nerium Oleander*, has leaves extraordinarily variable in size, the smallest being bractlike and only 0.027 the area of the largest ones. It did not seem possible to make satisfactory estimates of the relative areas of the sun leaves and shade leaves of this species.

All other species examined had shade leaves larger than their sun leaves. Exact measurements were made for only four species of these, as follows:

	Ratio of areas Sun÷shade
Citrus Aurantium	0.75
Olea europaea	0.56
Quercus Ilex (large tree)	0.44
Q. Ilex (small bushy sapling)	0.20
Rhamnus Alaternus	0.68

The comparisons were based on fairly typical twigs of the same age, and all the leaves of each twig, or an equal number of homologously situated leaves from each, were examined.

The shapes of the two classes of leaves in question were often found to differ widely. The ratio of length to breadth for the blades of the leaves was examined in ten species. In the pinnately compound leaves of *Pistacia Lentiscus* there was little difference in the ratios of sun leaves and shade leaves, whether leaf was compared with leaf or leaflet with leaflet. The other nine species gave the following results:

		Ratio length÷breadth	
		Sun	Shade
(1)	Arbutus Andrachne	2.70	2.35
(2)	A. Unedo	3.16	3.21
(3)	Buxus sempervirens	1.97	1.89
(4)	Citrus Aurantium	2.04	1.37
(5)	Myrtus communis tarentina	2.21	2.14
(6)	Nerium Oleander	5.90	5.34
(7)	Olea europaea	4.05	2.64
(8)	Quercus Ilex (large tree) A	2.69	1.60
	Q. Ilex (small bushy sapling) B	2.04	1.37
(9)	Rhamnus Alaternus	1.75	2.05

5 *Loc. cit.*, p. 351. 6 *Loc. cit.*, p. 304.

It was not possible in every case to obtain the per cent. of total illumination for the shade leaves examined. Those noted were as follows: (4) 2.8, (6) 2.2, (7) 4.6, (8)A 1.8, (8)B 1.1, (9) 4.6.

It is obvious from inspection of the results obtained that the sun leaves are usually narrower than the shade leaves in proportion to their length. This is especially true of the leaves of Citrus, Olea, and Quercus; and the Olea and Quercus are certainly among the most xerophytic of the nine species in the list above given. *Figs. 1–5* sufficiently illustrate the difference in form of the leaves in question.

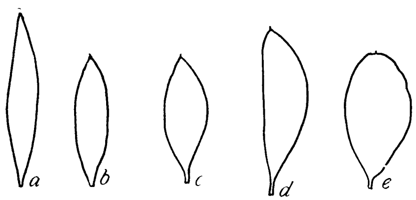

FIG. 1.—Leaves of *Olea europaea: A*, sun leaf of very xerophytic form; *B*, sun leaf; *C*, shade leaf from another tree; *D*, sun leaf; *E*, shade leaf from another tree which is in constant partial shade. ×0.4.

Another difference between the sun leaves and the shade leaves of many species consists in the manner in which the margins of the former are recurved. In many instances the under leaf surface of sun leaves is strongly concave, while that of shade leaves is nearly plane. This is well shown in the cross sections of *fig. 6*.

In the case of Olea the sun leaves and shade leaves differ remarkably in the manner in which they present their surfaces to the light. The latter are arranged in a somewhat horizontal manner, that is with the lower surface approximately parallel to the ground. But the former in many instances stand with the tips pointing almost straight upward or downward. In other words, the shade leaves are approximately euphotometric and the sun leaves panphotometric. It does not appear that the edges of the leaves are presented in a north and south direction more frequently than toward other points of the

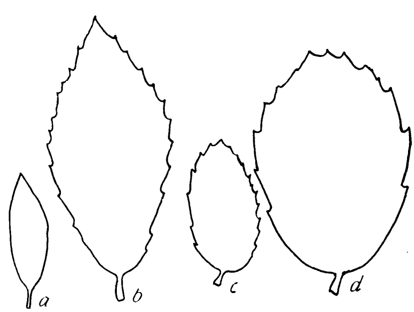

FIG. 2.—Leaves of *Quercus Ilex: A*, sun leaf, very small xerophytic form; *B*, shade leaf, same tree; *C*, sun leaf; *D*, shade leaf from another tree. ×0.4.

compass. It is this approximately vertical position of many leaves, with the silvery under surfaces facing in all directions, that gives the shimmering effect of olive foliage so often described. *Figs.* 7 and 8 illustrate extreme cases of leaves standing vertically as above described.[7]

The thickness of sun leaves was in every case found to be greater than that of shade leaves, as described by STAHL and others. In leaves of Quercus the ratio in thickness of the former to the latter was nearly 2.0; in Olea from 1.5 to 2.3; and in Pistacia from 1.8 to 3.7.

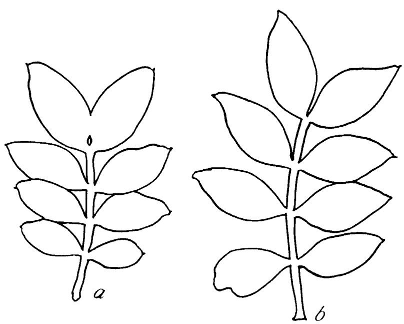

FIG. 3.—Leaves of *Pistacia Lentiscus:* *A*, sun leaf; *B*, shade leaf. ×0.4.

In those species which are pubescent or scaly on the lower surface the pubescence is much denser on sun leaves. It is generally difficult to reduce the comparison in this regard to a numerical basis, but an approximation of the kind can be made in the case of the leaves of Olea. The lower surface of the leaf is always more or less completely covered with peltate scales. On sun leaves the lower surface is so thickly scale-clad that the scales overlap considerably.

Apparently on sun leaves, the number of scales is sufficient to cover the under leaf-surface at least twice over. On some shade leaves the scales were found by measurements with the eyepiece micrometer to cover just one-quarter of the under surface, so that the scales were about one-eighth as numerous as on sun leaves.

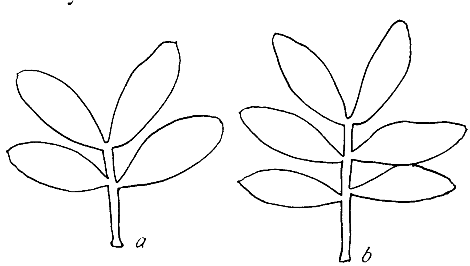

FIG. 4.—Leaves of *Pistacia Lentiscus* (another tree): *A*, sun leaf; *B*, shade leaf. ×0.4.

The stomata were found to be somewhat more numerous on sun leaves than on shade leaves; an average of two determinations gave 15 per cent. excess for the former.

[7] For these drawings the writer is indebted to Mrs. Herbert S. Jennings.

In none of the species studied were any such extreme differences between the internal structure of sun leaves and shade leaves noted as have been described by STAHL and others. Since the thickness and texture of the leaves of Pistacia differed more under different amounts of illumination than did those of any other species examined, special attention was paid to the histology of these leaves. The following points of difference, many of which can be verified by reference to *figs. 9–11*,[8] were made out: (1) cutinized layer of upper epidermis much more developed in sun leaves; (2) palisade layer double in sun leaves and single in shade leaves, the cells next the epidermis longer in the former; (3) intercellular spaces smaller in upper portions of mesophyll of sun leaves; (4) bundles much more highly developed in sun leaves; (5) a palisade layer occasionally developed next the lower epidermis in sun leaves.

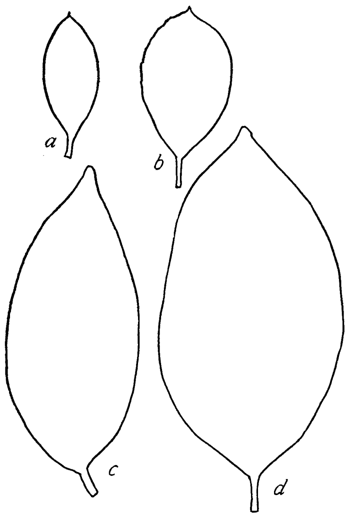

FIG. 5.—Leaves of *Rhamnus Alaternus* and *Citrus Aurantium:*, *A*, sun leaf, and *B*, shade leaf of Rhamnus; *C*, sun leaf, and *D*, shade leaf of Citrus. ×0.4.

II. RELATIVE AMOUNT OF TRANSPIRATION OF SUN LEAVES AND SHADE LEAVES.

The three most obvious cases which present themselves for investigation are: (*a*) transpiration of both kinds of leaves, each in its natural environment; (*b*) transpiration of both kinds in full sunlight; (*c*) transpiration of both kinds in shade.

No mode of determining the losses by transpiration of such leaves as those in question is free from sources of error. The plan of weighing detached leaves, with the cut end of the petiole sealed to prevent accidental loss, is an admirable one for succulent leaves. But for leaves with a less amount of stored water it is undesirable, because

[8] For these drawings the author is indebted to Dr. Grace E. Cooley, of Wellesley College.

the transpiration of the sun leaf and the shade leaf would be measured for unequal and rapidly diminishing amounts of contained water. Weighing whole plants growing in sealed pots is out of the question for large shrubs or trees, since seedlings which were small enough to be handled would fail to shade their own leaves and would not

FIG. 6.—Transverse sections of leaves: *A*, sun leaf, and *B*, shade leaf of Olea; *C*, sun leaf, *D*, shade leaf of *Quercus Ilex*. Natural size.

furnish leaves of typical adult form, size, and structure. Weighing leafy twigs with the cut ends immersed in water is not likely to afford the same absolute amounts of loss by transpiration as would be given by the same twigs supplied with water by the normal root pressure

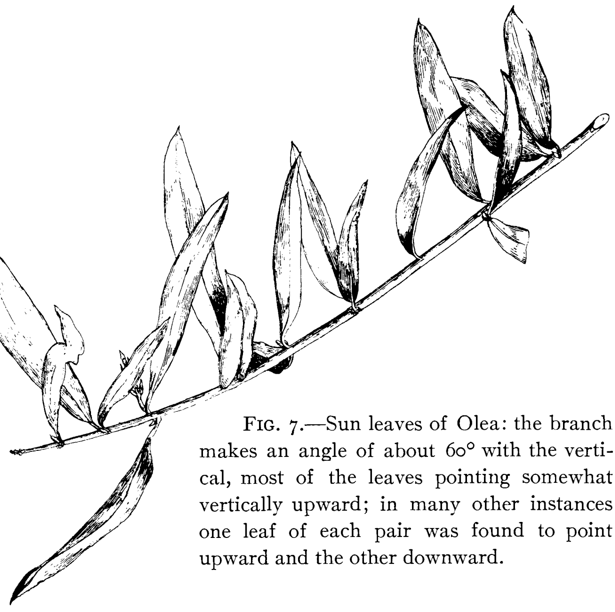

FIG. 7.—Sun leaves of Olea: the branch makes an angle of about 60° with the vertical, most of the leaves pointing somewhat vertically upward; in many other instances one leaf of each pair was found to point upward and the other downward.

of the plant. But the leaves are in a normal atmosphere, and their relative losses (as compared with each other) may be very nearly the same as under absolutely natural conditions.

The plan adopted in the experiments here recorded was to immerse the freshly cut ends of the leafy twigs studied in water contained in

small test tubes. Each stem was carefully sealed into its tube, but a capillary glass tube alongside the stem permitted air to enter to take the place of absorbed water. To show how much of the total loss was due to the cortex, control experiments were made with twigs deprived of their leaves. As it was found that the losses through the cortex sometimes amounted to 15 per cent. of those through the leaves, the plan of covering the entire cortical surface with cacao wax (a mixture of half beeswax and half cacao butter) was finally adopted. Weighings were made on a balance sensitive to less than 5^{mg} and the period in most cases allowed for transpiration (two to four hours) usually secured a loss of weight of more than 200^{mg} for the least active set of leaves employed. Only sunny days were chosen for the observations, which were all made out of doors. The thermometer ranged, during the season of the experiments and the hours of the day occupied by them, from 18 to 30° (usually from 20° to 25°). Most of the work was done between 12:00 and 5:00 P. M., and the per cent. of relative humidity at 3:00 P. M. was usually under 55. The determination of the per cent. of total illumination under which shade leaves have been developed seems to me an important part of any set of observations on the form, structure, or functional activity of such leaves, and many photometric observations were made on the leaves here discussed. Unless otherwise indicated, the per cents. given are for the illumination at or near midday, at the season stated. In general the shade leaves studied had grown in about the following amounts of illumination: Quercus, 1.5–5 per cent.; Olea, 4–6 per cent.;

FIG. 8.—Sun leaves of Olea: the branch stands nearly vertical and the leaves in general point upward.

Pistacia, 1–4 per cent.; Rhamnus, 4–6 per cent. The results of the determinations of comparative transpiration are as follows:

	Ratios $\frac{\text{Loss of Sun Leaves}}{\text{Loss of Shade Leaves}}$			
	Olea	Pistacia	Q. Ilex	Rhamnus
I. Sun leaves in sun and shade leaves in shade.				
Maximum	3.04	4.60	10.70	7.00
Minimum	1.45	2.20	1.85	2.25
Average of all values obtained	2.10	3.70	6.35	5.91
II. Both kinds of leaves in full sunlight.				
Maximum	2.15	2.24	3.90	1.42
Minimum	1.17	1.00	0.96	0.52
Average of all values obtained	1.47	1.70	2.04	0.98
III. Both kinds of leaves in the shade.				
Maximum	0.97	2.58	2.70	2.61
Minimum	0.81	0.68	0.93	1.17
Average of all values obtained	0.90	1.87	1.86	1.86

Summing up the results of the experiments on comparative transpiration (taking into account some aberrant values not included in the table above given), the following conclusions may be stated:

1. Under the conditions normal for each class (I), sun leaves transpire from three to ten times as much as the shade leaves of the same species.

2. With both classes of leaves under abnormally equal conditions (II and III) the sun leaves of the species studied usually transpire more than one and one-half times as much as the shade leaves.[9]

3. Averaging the averages of II and III, it appears that the inequality of transpiration of sun leaves and shade leaves is about as manifest in sunshine as in the shade.

4. The thinnest and most poorly nourished shade leaves contrast much more sharply with sun leaves in their behavior than do other more normal leaves which have developed in the shade. This is the principal cause for the difference between maximum and minimum results, particularly noticeable in the transpiration of *Q. Ilex*.

[9] This result is quite at variance with what would probably be the *a priori* opinion of botanists generally, and directly contravenes the statement of Wiesner (Biologie der Pflanzen, 1902, p. 11).

5. Shade leaves exposed for some hours to full sunshine may, without showing any signs of wilting, become almost unable to transpire. For example, a *Q. Ilex* shade leaf that during two hours in sunlight transpired almost one-fourth as much as a sun leaf from the

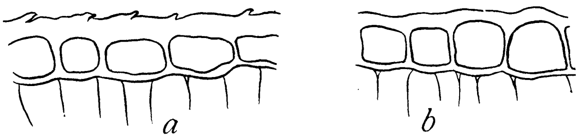

FIG. 9.—Upper epidermis of Pistacia: *A*, sun leaf; *B*, shade leaf. × 230.

same tree, was afterward in the shade found to transpire about one-sixtieth as much as the sun leaf in the shade.

The fact that shade leaves transpire less than sun leaves, under similar conditions, may at first sight appear singular. But a little consideration will suffice to show that leaves of the former class are structurally unable to perform as much of any kind of work as are

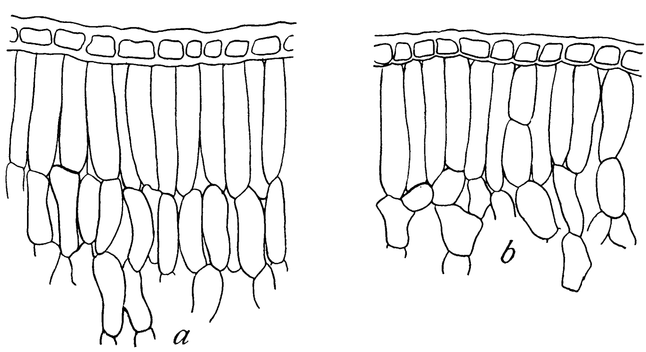

FIG. 10.—Upper epidermis and mesophyll of Pistacia: *A*, sun leaf; *B*, shade leaf. × 125.

the more vigorous sun leaves. The latter, by reason of the much stouter stems from which they spring, and the greater development of the bundles in the leaves themselves, are able to transfer in a peripheral direction larger quantities of water per unit of area per unit of time than shade leaves can. Also sun leaves, with a thickness two to four times that of shade leaves, usually contain much more interior evaporating surface than shade leaves of equal area.

These considerations, however, do not explain all of the observed inequalities of transpiration. Portions of leaves of *Agave americana* freshly cut and with the cut surfaces hermetically sealed with wax, so as to permit no loss of water except through uninjured epidermis, were found to give ratios ranging from 1.5 to 4 for loss of sun leaves compared with that of shade leaves, when both were exposed to full sunlight. Here the transportation of water is an unimportant factor, and the amount of tissue inside the leaf from which the transpired water is drawn was nearly the same in both cases. The Agave shade leaves had grown in a permanent shade of about 2 per cent. illumination.

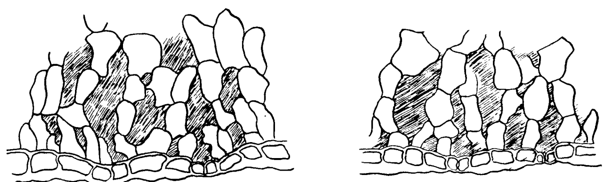

FIG. 11.—Lower epidermis and mesophyll of Pistacia: *A*, sun leaf; *B*, shade leaf. × 125.

It may be of interest to append a statement of the absolute rate of transpiration of the four trees and shrubs discussed in the table above given. The measurements were made with sun leaves a year old, at a temperature of 21° C. and a relative humidity of 67 per cent. The leaves were in moderately bright sunlight.

TRANSPIRATION IN MG. PER $100^{sq\,cm}$ LEAF SURFACE PER HOUR.[10]

Olea	302
Pistacia	231
Q. Ilex	238
Rhamnus	658

These are apparently large values for the transpiration of somewhat xerophytic plants. Leaves of *Ulmus campestris* and of *Pisum sativum* were examined at the same time, for purposes of comparison, and were found to lose 342 and 353^{mg} of water per hour, respectively. This, however, only serves to emphasize a fact too often lost sight of,

[10] Only one surface of each leaf (the lower) is taken into account.

namely that *xerophytic leaf structure is not always incompatible with abundant transpiration, but sometimes exists only for use in emergencies to protect the plant from injurious loss of water.*

In conclusion, the writer can only express his regret that he has so far been able to investigate only one phase of the transpiration of four out of some sixty coriaceous evergreen species which occur in the Mediterranean region. A detailed study of their transpirational activity, month by month throughout the year, could not fail to give results of much value.

NAPLES, ITALY.